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THE RIDDLE OF *OXYRUNCUS*

BY FRANK M. CHAPMAN

Oxyruncus is a genus of birds containing but one species (*O. cristatus*) with six closely related subspecies which, at more or less widely separated localities, are distributed from Costa Rica to Paraguay. The stability and persistence of the species are shown by its evident power to resist the factors to which its near allies have succumbed. *Oxyruncus*, therefore, has no close relatives and its exact position in our system of classification has never been satisfactorily determined.

Mt. Roraima, at the junction of Venezuela, British Guiana and Brazil, is the home of one of the forms of *Oxyruncus* (*O. c. hypoglaucus*). When, therefore, the recent Phelps Expedition to Venezuela secured nine specimens of *Oxyruncus* on Mt. Auyan-tepui, within 150 miles of Roraima, we supposed that they would, of course, be referable to the Roraiman form, but, greatly to our surprise, they prove to be separable. In a recently acquired collection from the Rio Tocantins, a locality whence *Oxyruncus* has not before been recorded, we have been further surprised to discover a second undescribed race of this species. Examination of our fifty specimens of the group, incident to the determination of these two apparently new forms, has led to certain conclusions which seem of sufficient general interest to warrant presentation apart from a paper on the zonal birds of the Auyan-tepui collection now in preparation. In order that they may be more conveniently referred to, I will first describe the proposed new forms:

Oxyruncus cristatus phelpsi,[1] new subspecies

SUBSPECIFIC CHARACTERS.—Intermediate between *Oxyruncus cristatus hypoglaucus* (Salvin and Godman) of Roraima, and *Oxyruncus cristatus brooksi* Bangs and Barbour of eastern Panama. Similar to the former above, similar to the latter below, differing from *hypoglaucus* in the whiter more heavily marked under parts, differing from *brooksi* in the darker green of the upper parts.

Four males, wing 92–93 mm.; tail 59–62 mm. Two females, wing 89, 95 mm.; tail 56, 61 mm.

TYPE.—Adult male. No. 305,638, American Museum of Natural History. Mt. Auyan-tepui, Venezuela, 1100 m. December 18, 1937; Wm. H. Phelps.

The color of the partly concealed crest in the 9 Auyan-tepui specimens is scarlet-red whereas the color in 9 Roraima specimens is flame-scarlet (Ridgway). Evidently this difference is due to fading in the older, Roraima skins. I find the same difference in color of the crest in two recently collected specimens of *Oxyruncus cristatus cristatus* from Santa Catharina and 12 old skins of this subspecies from the Rio region of Brazil. In our two specimens of *brooksi*, collected in 1915, the crest has apparently already faded since it resembles in color that of the old Whitely (1884) specimens of *hypoglaucus* from Roraima.

Just as this paper was completed Mr. Rudyerd Boulton, Curator of Birds in the Field Museum, informed me that they had recently received four specimens of *Oxyruncus* collected by E. R. Blake, Assistant Curator, on the British Guiana-Brazil boundary, a new locality in the recorded range of the species. I have been permitted to examine these birds. They prove to be referable to *phelpsi* rather than to the geographically nearer *hypoglaucus* of Roraima. The significance of this unexpected relationship may be revealed by Mr. Blake's collections.

In examining the specimens of this genus contained in our collection I find 5 specimens collected by A. M. Olalla at Baião on the lower Rio Tocantins in Brazil, whence the species has not before been

[1] I have named this unusually interesting new form in honor of William H. Phelps who has so long been a student of Venezuelan birds, and who collected seven of the Auyan-tepui series.

reported. This form is apparently undescribed. Like *phelpsi* it is a representative of the white-breasted, rather than of the yellow-breasted group. I propose for it the name

Oxyruncus cristatus tocantinsi, new subspecies

SUBSPECIFIC CHARACTERS.—Nearest to *Oxyruncus cristatus hypoglaucus* of Roraima but smaller, the under parts slightly paler, the black marks less pronounced, and more rounded. Three males, wing 86–89 mm.; tail 54–60; culmen 14–15 mm.

TYPE.—Adult male. No. 431,219, American Museum of Natural History. Baião, Pedral, Rio Tocantins, Brazil. December 16, 1931; collector, A. M. Olalla.

The fact that *Oxyruncus* has not before been recorded from Amazonia makes it surprising that we should receive 5 specimens from a known collecting locality in what may be called the Snethlage area. When we discover that all 5 birds were collected on the same day (Dec. 16, 1931) we conclude that the species is not only very rare but very local in this region.

With the exception of Paraguay, Baião is the only non-mountainous region whence *Oxyruncus* is known.

SPECIMENS EXAMINED

Oxyruncus cristatus cristatus.—BRAZIL: "Brazil" (Rothschild Collection), 10; Minas Geraës, 3; São Paulo, 5; Santa Catharina, 2. PARAGUAY: 1.

Oxyruncus cristatus frater.—COSTA RICA: "Costa Rica," 1; Carrillo, 2; Bonilla, 1.

Oxyruncus cristatus hypoglaucus.—VENEZUELA: Roraima, 7; BRITISH GUIANA: Merume Mts., 1; Rio Caramang, 1.

Oxyruncus cristatus brooksi.—EASTERN PANAMA: Tacarcuna, 2400 ft., 1; 4200 ft., 1.

Oxyruncus cristatus phelpsi.—VENEZUELA: Mt. Auyan-tepui, 1100 m., 9. BRITISH GUIANA: Brazil boundary, 4.

Oxyruncus cristatus tocantinsi.—BRAZIL: Rio Tocantins, 5.

DISCUSSION

Consideration of the factual evidence presented in the preceding summary indicates primarily that *Oxyruncus* is a relict species approaching extinction. Presumably it once occupied favorable territory throughout the vast area included between the ranges of its peripheral forms in Costa Rica and Paraguay. Today it is known, additionally, only from eastern Panama, the Roraima region, the British Guiana-Brazil boundary and the lower Tocantins.

The six slightly differentiated races of the species fall into two groups, one of which is yellow, the other white, yellow-tinged below. The "yellow" group contains:

1. *Oxyruncus cristatus frater*—Costa Rica and western Panama.
2. *Oxyruncus cristatus cristatus*—southeastern Brazil; Paraguay.

The white group contains:

3. *Oxyruncus cristatus hypoglaucus*—Roraima; western Guiana.
4. *Oxyruncus cristatus phelpsi*—Mt. Auyan-tepui; British Guiana-Brazil boundary.
5. *Oxyruncus cristatus brooksi*—eastern Panama.
6. *Oxyruncus cristatus tocantinsi*—Rio Tocantins, Brazil.

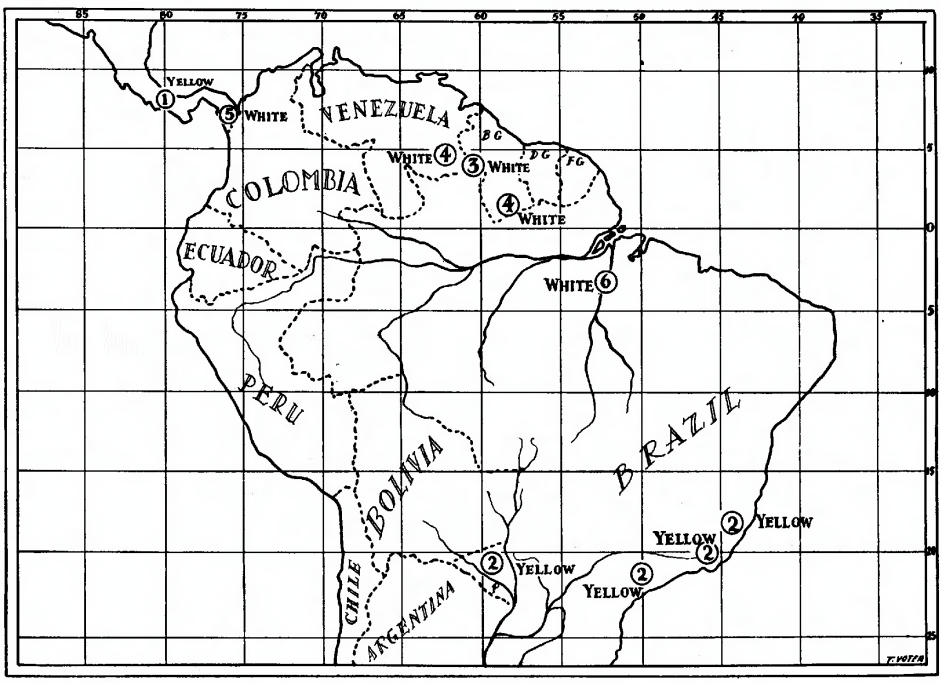
Before attempting to explain the origin and distribution of these six races we should remember that they are the closely allied representatives of a single species and that, fundamentally, the history of one is the history of all.

The key to our problem lies in discovering their center of dispersal. Whence came these birds? Are they expressions of their current environment or did they evolve elsewhere? For example, are the almost identical yellow-breasted races at the periphery of the range of the species, in Costa Rica and Paraguay, the product of parallelism or have they descended from a common, yellow-breasted ancestor? The fact that they more closely resemble each other than they do the forms geographically nearest to them, in connection with their stability in the areas they occupy, discourages the belief that separately they have independently developed similar characters. Other factors also lead us to reject parallelism as an explanation of their resemblance and we turn to Matthew's[1] theory of the origin of peripheral forms at their center of dispersal as pertinent in this connection. Matthew writes (p. 10):

"Whatever agencies may be assigned as

[1] William Diller Matthew, Climate and Evolution, Second Edition, Special Pub. N. Y. Acad. Sciences, I, 1939.

the cause of evolution of a race, it should be at first most progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it."



The Distribution of *Oxyruncus*

1. *Oxyruncus cristatus frater*
2. " " *cristatus*
3. " " *hypoglaucus*
4. *Oxyruncus cristatus phelpsi*
5. " " *brooksi*
6. " " *tocantinsi*

Again (p. 32): "Whatever be the causes of evolution, we must expect them to act with maximum force in some one region; and so long as the evolution is progressing steadily in one direction, we should expect them to continue to act with maximum force in that region. This point then will be the center of dispersal of the race. At any given period, the most advanced and progressive species of the race will be those inhabiting that region; the most primitive and unprogressive species will be those remote from this center."

Accepting Matthew's views as applicable to our case it remains for us to discover where *Oxyruncus* originated and whence it radiated. The existing evidence points to the Roraima region as this center of dispersal. It is situated in the heart of the known range of the group. The species is not uncommon there (the Phelps Expedition secured nine specimens on Auyantepui) and the occurrence of two forms within a limited area indicates that it is or was a region of active speciation. Moreover, the Roraiman district has experienced the environmental changes which would provide an impulse to range extension and also to evolutionary development. The existing environment tells an eloquent story of the action of forces which have transformed a high, extended tableland into low-lying savannas and tropical forests set with flat-topped mountains on whose higher altitudes still remain relicts of the life that once characterized the area of which they formed a part.

In brief, the Roraima region meets the requirements of a center of dispersal and

we may think of the common ancestor of the yellow-breasted *Oxyruncus* as inhabiting its former tablelands. Thence, either before or induced by the changes to which I have referred, it extended its range northward at least to Costa Rica and southward as far as Paraguay. The individuals of the species remaining, responding to changing environmental conditions, evolved from yellow-breasted to white-breasted forms and the continued radiation of the species from this common center is proved by the presence of white-breasted forms in eastern Panama and on the Rio Tocantins. As a theoretical resident of the Roraiman tableland *Oxyruncus* must have been a subtropical species and we may assume that its extensions of range, northward as well as southward, were performed under climatic conditions which brought lower temperatures to the Tropical Zone. The distribution of birds furnishes abundant evidence of the existence of such a climatic factor in this region. At one time, therefore, it is probable that *Oxyruncus* was more or less continuously distributed between the extremes of its present range. But with the return of the higher temperatures that mark the now existing climate it yielded to the unfavorable conditions of lower altitudes and has continued to exist only where altitude or latitude, or both combined, give it a more or less subtropical environment.

Today the small form recently discovered on the Rio Tocantins is the only one known from a non-mountainous locality in the tropics.

Reviewing this attempt to interpret the evidence presented by our specimens of *Oxyruncus*, I find that at the best I have merely moved the outlying yellow-breasted form from the margin, to the heart of its range. To the question whence came this theoretical inhabitant of the former Roraiman tableland I have no answer. If we have no means to measure the time represented by its recorded history, how incredibly remote must have been its beginnings!